POST-NINE WEEK EFFECTS OF UNILATERAL INCISIONS OF THE CEREBRAL HEMISPHERES OF *TRITURUS VIRIDESCENS*

A THESIS

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THE DEGREE OF MASTER OF SCIENCE

BY

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DEDICATION

To my mother and father, whose love inspired the undertaking of my advanced training, whose understanding sustained me during the difficult days I was in pursuit of this training, and whose sacrifices have made the completion of this training possible.

ACKNOWLEDGMENTS

I am very grateful to Miss F. M. Whitehurst, my adviser, and Dr. M. L. Reddick, Chairman of the Department of Biology, Atlanta University, for their understanding, encouragement and helpful criticisms during the process of this study.

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CHAPTER I

INTRODUCTION

Most of our knowledge regarding the regenerative capacity of the amphibian central nervous system has been derived chiefly from experiments on the embryonic neural axis and from observations on the restoration of the spinal cord following transection. Detwiler ('44, '46, '47) observed that unilateral extirpation of the embryonic medulla, midbrain and the brachial region of the spinal cord of Amblystoma was followed by restitution from the intact opposite half. It has been shown by Hooker ('15, '25) that simple transection of the embryonic spinal cord in the frog resulted in perfect healing and regeneration. There have been relatively few investigations on regeneration of the adult amphibian central nervous system. Piatt ('55a) was able to demonstrate fiber regeneration of the spinal cord of adult Triturus pyrrhogaster. In an earlier study, according to Piatt (55b), Sibbing observed that following unilateral extirpation of the cerebral hemispheres very little regeneration occurred.

Plump ('59) investigated the problem of regeneration in the cerebral hemispheres of adult Triturus viridescens. In his investigation, animals were observed at intervals of from 24 hrs. to 9 weeks. The results of his experiments indicated that regeneration in the cerebral hemispheres of adult Triturus viridescens did not occur within this period of time. These results inspired the writer of this thesis to further the investigation of this problem so as to examine the possibility of regeneration within a 13 week period.

CHAPTER II

REVIEW OF LITERATURE

Pearcy and Koppanyi ('24) transected the spinal cord of the adult goldfish, Carassius auratus, in the cervical region. Immediately following the operation it was noted that there was a paralysis of the body behind the lesion. After 6 weeks swimming movements were observed in the region behind the transection. These movements became more frequent and at the end of two and one-half months the animals' swimming movements became normal (constant coordination between the anterior and posterior parts of the body). It was thus concluded that functional recovery had taken place.

Keil ('40) tested the capacity of the spinal cords of teleosts to regenerate. He transected the cords of adult rainbow fish. After 24 hrs. the transected animals were observed and tested for reflexes at 24 and 48 hour intervals, for as long as 41 days. From these observations it was found that there existed a paralysis of the body behind the level of the lesion. Return of function was evidenced by the appearance of an occasional flexion of the tail and normal spreading of the caudal fin. These activities gradually became more constant and coordinated and eventually approached those of the normal fish.

Hooker ('32) cut across the spinal cord of the young rainbow fish, Lebistes reticulatus. These cuts were made at the level of the anterior end of the dorsal fin within the first 4 days after "birth". Upon immediate stimulation it was observed that, in some animals, the body behind the cut was paralyzed. Three days following spinal section the space between the cut cord ends was filled with a mass of nerve fibers which grew from both wound surfaces of the cord, however, these fibers did not enter the opposite

ends of the cords. Four days after the operation movements of the dorsal and tail fins were elicited (beginning of nervous transmission). These movements became progressively more synchronous with those of the trunk. At this same time most of the nerve fibers which grew from both wound surfaces of the cord were observed to have entered the opposite end. By the 5th or 6th day following the section the locomotion of these animals differed in no way from the locomotion of the normal ones. Thus it was demonstrated that both functional and morphological regeneration of the spinal cord of young rainbow fish occurred.

Tuge and Hanzawa ('37) sectioned the spinal cord of adult teleosts, the Japanese rice minnow, in the cervical region. Following the operation, it was noted that these animals could be distinguished from the normal animals in four ways: (a) motor paralysis of the body behind the lesion (disappearance of rhythmic tail movements); (b) presence of spinal reflexes of the tail and fins behind the lesion; (c) disappearance of rhythmic movement of the caudal fin, and (d) lowered muscle tone in all of the fins except the pectoral fins. Morphologically, the regenerative process was observed to begin with the outgrowth of fibers from motor cells in the tracts of the uninjured portions of the cord. After 10 days functional restitution was observed, however, these animals were not completely normal since there still existed a partial loss of muscle tone of the fins. After 8 weeks the form and structure of the regenerated area had become reestablished.

Hooker ('15) transected the spinal cord of tadpoles of Rana sylvatica and Rana catesbiana during the tail bud and hindlimb stages. The operation consisted of complete transection of the spinal cord and notochord in the cervical region. According to Hooker, regeneration was accomplished by: (a) the outgrowth of nerve fibers from the motor cells in each segment of the

cord; (b) the growth of sensory axons from the cut surface of the posterior stump, and (c) the elongation of both ends of the transected cord toward each other by proliferation of the ependymal cells of the central canal. Histologically, it was thus shown that the spinal cord of frog embryos regenerated after being completely severed in the cervical region during the tail bud and hindlimb stages.

Hooker ('25) made a later study of spinal cord regeneration in tadpoles of Rana sylvatica. He completely transected the cords in the cervical region during the tail bud and hindlimb stages. From microscopic examinations made from 20 days to three months after the transection, Hooker observed: (a) the outgrowth, from both ends of the transected cord, of nerve fibers which arose from nerve cells situated in the original cord; (b) the proliferation of the ependymal cells of the central canal of the old cord until the central canal of the new cord was reestablished, and (c) the proliferation of indifferent cells in the original cord. These indifferent cells were believed to migrate and differentiate into neuroblasts and spongioblasts which assisted in the restitution of the gray matter. Hooker concluded that, under the conditions of these experiments, the gross form and normal structure of the cord of frog tadpoles were restored.

Detwiler ('47) excised the right half of the presumptive brachial region of the spinal cord from Amblystoma embryos following the closure of the neural folds. Histologically, he observed that the regenerative processes consisted of excessive cellular proliferation and migration of cells from the intact contralateral half of the brachial region to the region of the injury. This was augmented by proliferation of ependymal cells of the central canal. These observations revealed that following excision of the right half of the presumptive brachial region of the spinal cord in Amblystoma resulted in

complete restitution.

Piatt ('55a) studied spinal cord regeneration in adult Triturus pyrrhogaster. The cords were completely transected at a level approximately midway between the fore and hindlimbs. Anatomically, it was observed that by the 7th day the cut stumps were completely separated and that the gaps made by the cut were filled with blood cells, debris of nerve tissue and a plasma-like exudate. By the 10th day there appeared the first signs of fiber regeneration and by the 16th day many fibers were observed between the cut ends of the cords, several of which had bridged the complete distance between the cut ends. By the 20th day and thereafter fiber regeneration increased rapidly. The oldest regenerated cords did not attain a normal diameter through the region of the cut, but the central canals and the white matter were approximately normal in appearance. The cells constituting the gray matter throughout the regenerated region were reduced in number and at no stage in the process was proliferation of new nerve cells detected.

Smith ('58) made a study of the regenerative capacity of the spinal cord of the adult Triturus viridescens. He transected it in the cervical region. Observations were made morphologically and histologically from one to 10 weeks. He found that complete restoration of the cord occurred 6 weeks after the transection.

Clearwaters ('54) transected the spinal cords of chick embryos of two to 5 days of incubation and of chicks a few days after hatching in order to determine their regenerative capacity. In the chick embryos it was observed that the first step in the regeneration of the spinal cords consisted of the rounding off of the cut ends. This was followed by the growth of nerve fibers from the cut surfaces. The process of regeneration did not begin before the second day after the operation and it was practically completed by the

14th day. In the chicks which were operated upon after hatching there were some indications of nerve fiber regeneration by the 5th week, however, it was doubtful if any neurons had crossed the scarred area between the cut ends of the cords. It was concluded that regeneration occurred in chick embryos in which the spinal cords were transected after two to 5 days of incubation and that essentially no regeneration occurred in chicks operated upon after hatching.

Weissfeiler ('24) excised one or two olfactory lobes, with or without destruction of one of the corresponding cerebral hemispheres of axolotls and tritons. He demonstrated that regeneration occurred first by the formation of an enlargement or bulb of regeneration which contained neuroblasts. These neuroblasts gave rise to a thin tractus that entered into relationship with the corresponding hemispheres. This was followed by a more intense production of fibers and cells after which there was a differentiation and separation of the cellular and fibrous layers. He further demonstrated that the pia-mater played an important role in the regenerative process. It regenerated first and more rapidly than nerve elements and formed an ocrea which served as a guide for the newly-formed olfactory fibers. When the ocrea was destroyed, the regeneration of the cylindraxes still occurred but they were malformed and brought about an abnormal union of the olfactory bulbs with the cerebral hemispheres.

Detwiler ('44) removed the right walls of the medulla from embryos of Amblystoma punctatum. It was observed, from his histological sections, that following the operation there was a gradual restitution of the excised walls from the intact contralateral walls. This was accomplished by extensive proliferation and migration of extra-ependymal cells from the intact side to the opposite side. At the end of the regenerative process the walls appeared

structurally complete and normal except for the absence of Mauthner's cells and a reduction in size of the median longitudinal fasciculus on the intact side. These results demonstrated, according to Detwiler, that one (unilateral) half of the medulla is totipotent for the whole, in embryos of Amblystoma punctatum.

Detwiler ('45) studied Amblystoma larvae in which the forebrain had been unilaterally and bilaterally extirpated. In addition to the forebrain, these operations included the removal of the presumptive nasal placodes and the rudiments of the eyes. He found that larvae devoid of cerebral hemispheres, eyes and nasal sacs were able to lead an autonomous existance and that motor activities concerned with lurching, engulfing food, chewing and swallowing were carried out in an integrated manner, but less vigorous than in larvae with intact hemispheres. It was observed that spontaneous behavior was greatly reduced, especially the foraging reactions. He also observed that when the right half of the forebrain, including the optic and olfactory rudiments, were removed no regeneration took place and that in the absence of one hemisphere and its adjacent olfactory end organ, the contralateral hemisphere underwent a marked compensatory increase in size which was due to cellular hyperplasia.

Detwiler ('46) used various stages of Amblystoma embryos and studied the regeneration of the mesencephalon. He found that unilateral excision of the midbrain was followed by a gradual restoration of the excised half. This restoration was observed to be completed by the 17th post-operative day at which time the midbrain was symmetrically normal as regards both cellular and fibrous regions.

Burr ('16) performed two series of operations on embryos of Amblystoma in which the peripheral nerves and the circulatory systems had not developed.

In the first series the right cerebral hemisphere and the right nasal placode were extirpated. In the second series the right telencephalon was removed, but the right nasal placode was left intact. According to Burr, the above operations subjected the brain tissue left by the extirpation of the hemisphere to two conditions. In the first series the nervous tissue was left to regenerate without the possibility of any stimulus from the end organ that was connected with it. In the second series the end organ and the nasal placode were left in their normal positions and therefore acted as a stimulus to the nervous tissue. In the first series of experiments wound healing usually was accomplished within the first 24 hrs. After 5 days a new wall had formed which connected the wall of the right diencephalon with the wall of the left telencephalon. This wall consisted at first of a narrow band of new cells, derived from ependymal cells, which bridged the interventricular foramen. As growth proceeded the narrow band of cells was drawn out into a thin plate, about two or three cells thick, which stretched across the foramen. In one of the larvae of the second series it was found that the new tissue was composed entirely of the typical columnar cells that make up the ependyma. As growth progressed the cells of the new membrane lost their columnar shape and metamorphosed into flatten quadrilateral cells. It was thus concluded that the regenerated portion was not made up of nerve cells but rather of cells from the primitive germinal epithelium which lined the neural tube. It was further concluded that the regeneration which took place was limited to that necessary to close the wound made by the removal of the hemisphere.

Sperry ('48) made a study of the regeneration of nerve fibers which mediate visuo-motor coordination in the adult newt. He completely transected the brain just anterior to the cerebellar commissures. He reported that nerve fibers grew into the area left by the cut and made anatomical connections,

after which visuo-motor coordination returned. From these observations it was concluded that regeneration of the brain of adult newts occurred when transected just anterior to the cerebellar commissures.

According to Piatt ('54), Sibbing made a study on regeneration of the brain in adult urodeles. He removed one or both cerebral hemispheres and large pieces of the hemispheres. He observed very little regeneration following the removal of one cerebral hemisphere and practically none when both hemispheres were removed. When only the olfactory bulb was excised reconstitution of the missing part was fairly complete.

Plump ('59) made a study of the regenerative capacity in the central nervous system of adult Triturus viridescens. He made unilateral incisions of the cerebral hemispheres in the rostral, middle or caudal regions. From histological studies, made at intervals of 24 hrs. to 9 weeks, he demonstrated that regeneration of the cerebral hemispheres in these animals did not occur. Although no regeneration was observed by Plump, healing of the integument over the wounded area was complete by the 7th week. It was further observed that there was a decrease in the size of the injured hemisphere and lumen while there was a corresponding increase in the size of the opposite hemisphere.

CHAPTER III

MATERIALS AND METHODS

The experimental animals used in this research were adult Triturus viridescens. During the pre-operative period the animals were kept in a balanced aquarium. At this same period the animals were fed on a diet which consisted only of Tenebrio larvae.

In preparing the animals for the operation a five-tenths per cent solution of chloretone was poured into two finger bowls to a level which would just cover the animals once they had been placed into the solution. The chloretone usually caused the cessation of all movements within 15 to 20 mins. At this point, the animals were ready for the operation.

The operation, on each animal, consisted of making an oblique incision on the right side just anterior to the eye through the epidermis, skull and the cerebral hemisphere. There was, however, no criteria by which to determine whether the incision passed through the brain. All of the incisions were made with iridectomy scissors which had been washed in 95% ethyl alcohol. Immediately following the operation the animals were placed in battery jars, which contained conditioned tap water, where they were kept until they were sacrificed. The animals were sacrificed at intervals of from 10 to 13 weeks. This was done by detaching the portion of the head containing the brain from the body of the animal. The detached portion was fixed for two days in Bouin's fixative solution. Upon removal of the detached portion from the fixative it was washed in several changes of 70% ethyl alcohol over a period of two days. At the end of this period it was placed in a decalcifying solution. Horizontal and transverse sections of from 10 to 15 u. were made. These sections were stained either with Protargol-S after Bodian ('36), or with iron hematoxylin.

CHAPTER IV

EXPERIMENTAL RESULTS

The following is a description of the histological observations of the intact and the operated cerebral hemispheres of the adult Triturus viridescens.

A Description of the Intact Cerebral Hemispheres.--The cerebral hemispheres are protected by three meningeal layers, the dura mater, arachnoid and the pia-mater. The cerebral hemispheres are distinctly divided into two layers. These are the external white matter and the internal gray matter (fig. 1). The white matter is chiefly composed of a few fibers from the olfactory tract. A few nerve cells can also be observed in this area. The gray matter is composed of two cellular layers: an outer, stratum of mitral cells and an inner, stratum granulare (fig. 2). These layers are easily distinguished from each other since the granule cells which make up the stratum granulare are smaller and more compact than the cells of the mitral layer (fig. 3). Both types of cells, however, have the same general appearance in that they are oval and contain granules within their nuclei. In sections of the entrance of the olfactory nerve into the olfactory bulb two other layers can be observed, the stratum nervosum and the stratum glomerulosum (fig. 4). The former is composed of fibers from the olfactory nerve and the latter is composed of the terminal ramifications of these fibers and the dendritic branches of the mitral cells.

In sections of the lateral ventricle ependymal cells of the columnar type can be seen lining the ventricles (fig. 5). The chorioid plexus which is composed of large cells with darkly stained nuclei can be observed within the lateral ventricles.

Post-nine week Description of the Cerebral Hemispheres following unilateral Incisions.--When microscopic examinationw were made it was found that

the incisions were located in either the rostral or middle regions of the right cerebral hemisphere. It was further found that the incisions had severed the hemisphere either partially or completely.

After 10 weeks, it was observed that the incision had severed the hemisphere at the anterior level of the lateral ventricle. Evidence of the site of incision was indicated by scattered nerve cells and a portion of the chorioid plexus lying between the severed edges of the hemisphere (fig. 6). It was further noted that there was a definite decrease in the size of the operated hemisphere and the lateral ventricle (fig. 7).

After 11 weeks, it was observed that the incision severed the rostral portion of the cerebral hemisphere at the level of the olfactory bulb where the olfactory nerve makes its entrance. The site of incision was evidenced by the presence of degenerative fiber debris and severed edges of white matter in the injured area (fig. 8). It was further noted that the injured hemisphere was smaller than the uninjured hemisphere (fig. 9).

After 12 weeks, it was observed that the incision severed the middle region of the hemisphere. The site of injury was evidenced by the presence of a gap which separated the rostral and caudal portions of the hemisphere. The gap was observed to vary in size with the level of the hemisphere from which the section was taken (figs. 10-12). The lateral ventricle of the injured side was observed, in dorsal sections, to be confined to the caudal region of the hemisphere (figs. 11 and 12). In more ventral sections, however, traces of the lateral ventricle could be observed in the rostral half of the hemisphere (fig. 13). Further ventrally, at the level of the interventricular foramen, the lateral ventricle of the injured hemisphere was continuous (fig. 14). It was observed that the injured hemisphere had decreased in size and that the stratum glomerulosum of the same side was less extensive than

that of the uninjured hemisphere (fig. 15).

After 13 weeks, it was observed that the incision severed the rostral portion of the hemisphere in the region of the olfactory bulb. The injured site was evidenced in dorsal sections by a gap which separated the olfactory bulb from the remainder of the hemisphere (fig. 16). In ventral sections the injured portion of the hemisphere was observed to be club-shaped (fig. 17). This condition gradually disappeared as the sections were traced more ventrally until the olfactory bulb was not observed (figs. 18-20). The injured area was filled with pieces of muscle tissue, nerve fibers and scattered nerve and neuroglial cells (figs. 18-22). The stratum glomerulosum of the injured hemisphere was less extensive than that of the opposite uninjured hemisphere (fig. 17). Fewer fibers were observed in the olfactory nerve in the operated hemisphere than in the unoperated hemisphere (fig. 17).

CHAPTER V

DISCUSSION

The results, under the conditions of this investigation, indicate that regeneration does not occur in the cerebral hemispheres of adult Triturus viridescens after unilateral incisions. This observation may be attributed to the following factors: (1) the 13 week period of experimentation was not long enough to allow the regenerative processes to begin; (2) the extent of the incisions was too great to allow regeneration to occur, and (3) the capacity for Triturus viridescens to regenerate may be lost in the adult stage.

In this investigation a reduction in the size of the injured hemisphere and its lumen was observed. This may have resulted from the degeneration of nerve fibers in the hemisphere. Plump ('59) observed that after unilateral incisions of the cerebral hemispheres of adult Triturus viridescens there was a reduction in the size of the injured hemisphere. He also observed that there was an increase in the size of the contralateral hemisphere which probably was due to cellular hyperplasia. Detwiler ('45) observed that following removal of the right forebrain along with its olfactory rudiments of Amblystoma larvae there was a marked compensatory enlargement of the contralateral hemisphere as a result of cellular hyperplasia. In this investigation there appeared to be a slight increase in the size of the uninjured hemisphere. This was not considered to be due to hyperplasia but rather to a variation in the sizes of the control and experimental animals.

CHAPTER VI

SUMMARY AND CONCLUSIONS

1. Oblique unilateral incisions were made with iridectomy scissors just anterior to the eye through the cerebral hemispheres of adult Triturus viridescens.

2. Microscopic examinations revealed that the incisions were located in either the rostral or middle regions of the right cerebral hemispheres.

3. The results, under the conditions of this investigation, indicated that regeneration did not occur in the cerebral hemispheres of adult Triturus viridescens after unilateral incisions.

4. It was observed that after unilateral incisions were made in the cerebral hemispheres of adult Triturus viridescens the injured hemisphere underwent a reduction in size.

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PLATE I

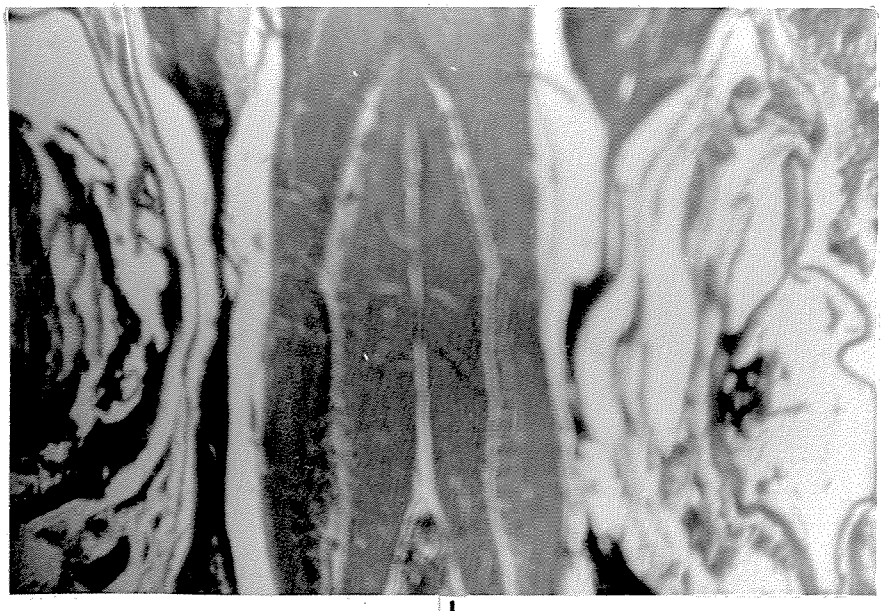
(Explanation of Figures)*

*All figures are photomicrographs.

(Explanation of Figures)

Fig. 1. A horizontal section of the cerebral hemispheres of Triturus viridescens (control). Observe the equality of the size of the two hemispheres. X 35.

Fig. 2. A horizontal section of the cerebral hemispheres (control). Observe the white and gray matter. X 100.



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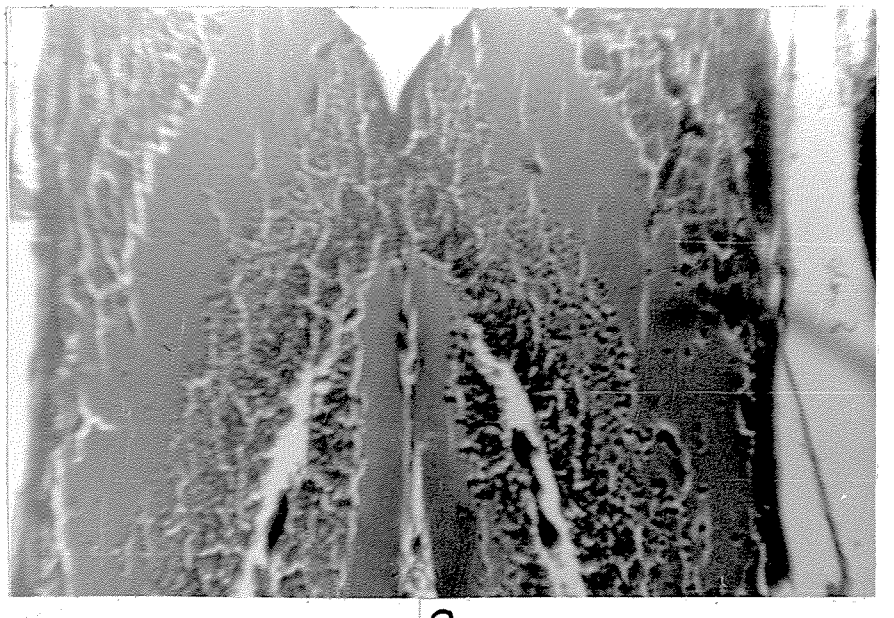

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PLATE II

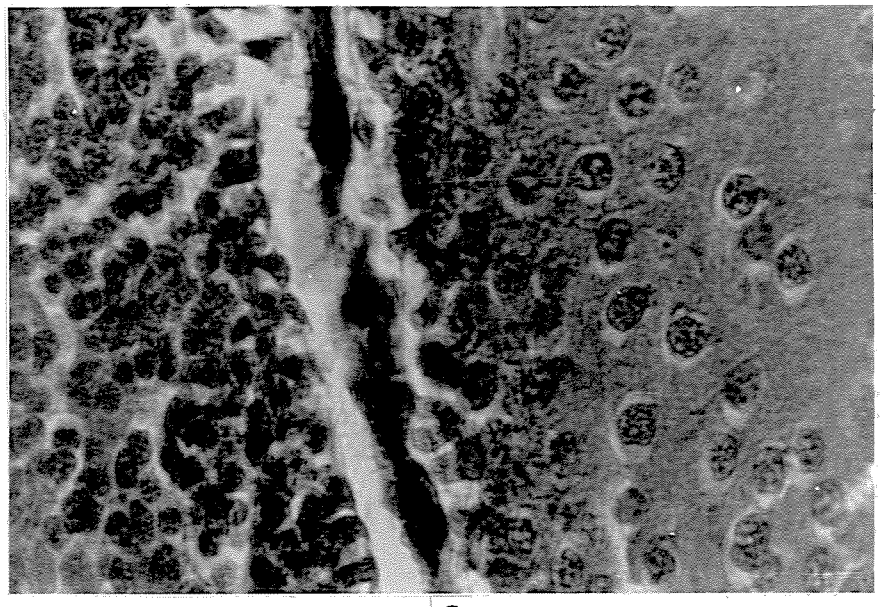
(Explanation of Figures)*

*All figures are photomicrographs

(Explanation of Figures)

Fig. 3. A horizontal section of the cerebral hemisphere of Triturus viridescens (control). Observe the granular and mitral cells and the chorioid plexus. X 430.

Fig. 4. A horizontal section of the cerebral hemispheres (control). Observe the stratum nervosum and the stratum glomerulosum. X 100.



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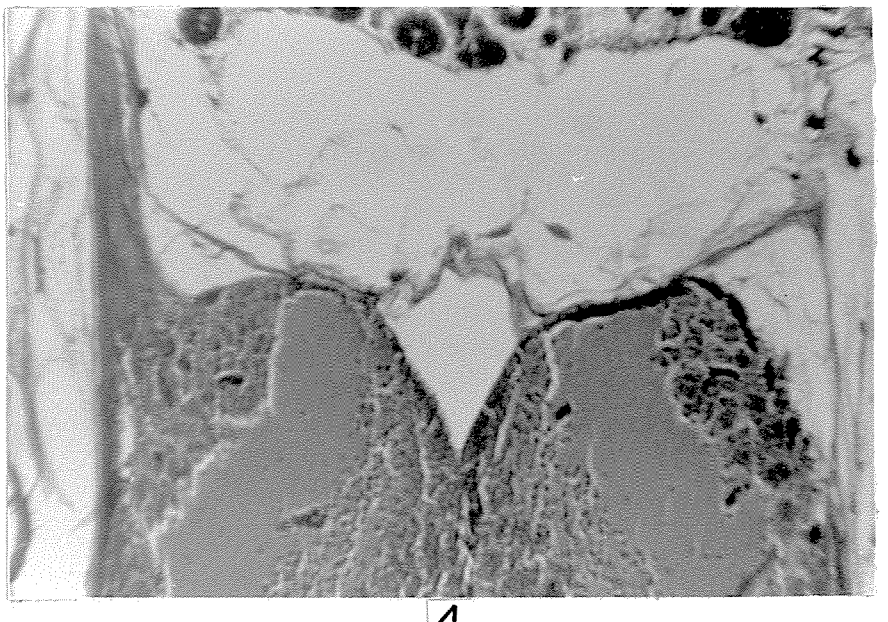

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PLATE III

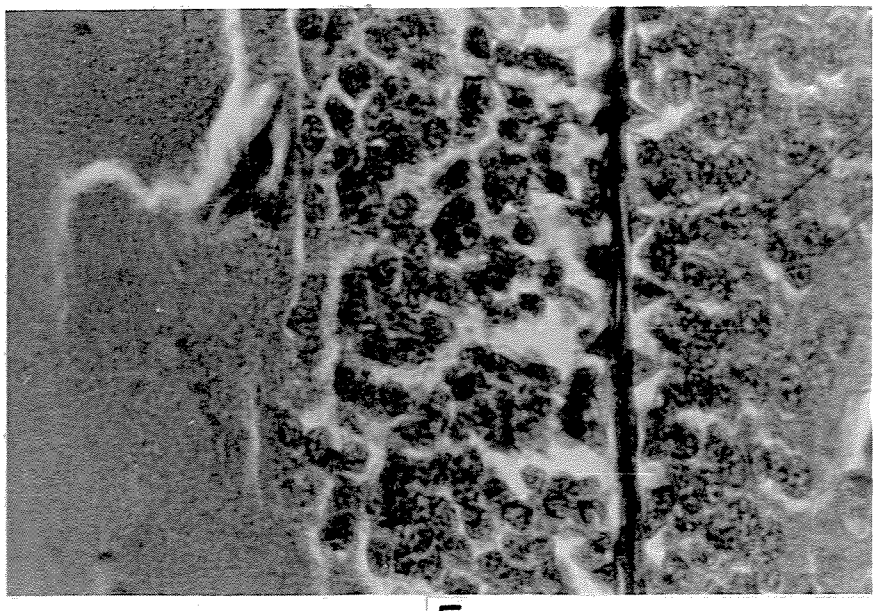
(Explanation of Figures)*

*All figures are photomicrographs.

(Explanation of Figures)

Fig. 5. A horizontal section of the cerebral hemisphere of Triturus viridescens (control). Observe the cells which line the lateral ventricle. X 430.

Fig. 6. A horizontal section of the injured hemisphere 10 weeks after unilateral incision. Observe the chorioid plexus and nerve cells in the injured area. X 430.



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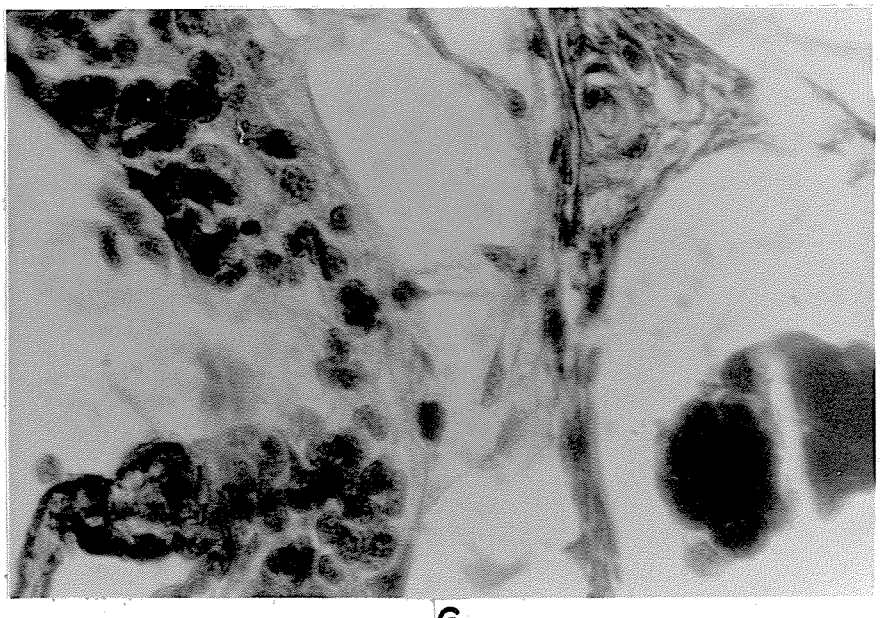

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PLATE IV

(Explanation of Figures)*

*All figures are photomicrographs.

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Fig. 7. A horizontal section of the cerebral hemispheres of Triturus viridescens 10 weeks after unilateral incision. Observe the size of the injured hemisphere and its lumen. X 35.

Fig. 8. A horizontal section of the cerebral hemispheres 11 weeks after unilateral incision. Observe the size of the injured hemisphere. X 35.

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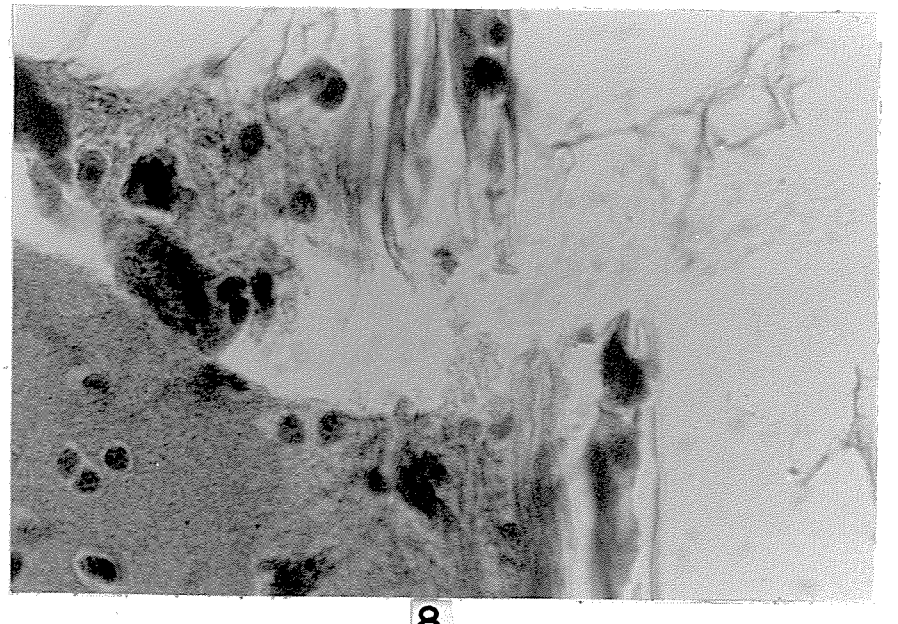

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PLATE V

(Explanation of Figures)*

*All figures are photomicrographs.

(Explanation of Figures)

Fig. 9. A horizontal section of the cerebral hemisphere of Triturus viridescens 11 weeks after unilateral incision. Observe the degenerative fiber debris in the injured area. X 430.

Fig. 10. A horizontal section of the cerebral hemispheres 12 weeks after unilateral incision. Observe the gap and size of the injured hemisphere. X 35.

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PLATE VI

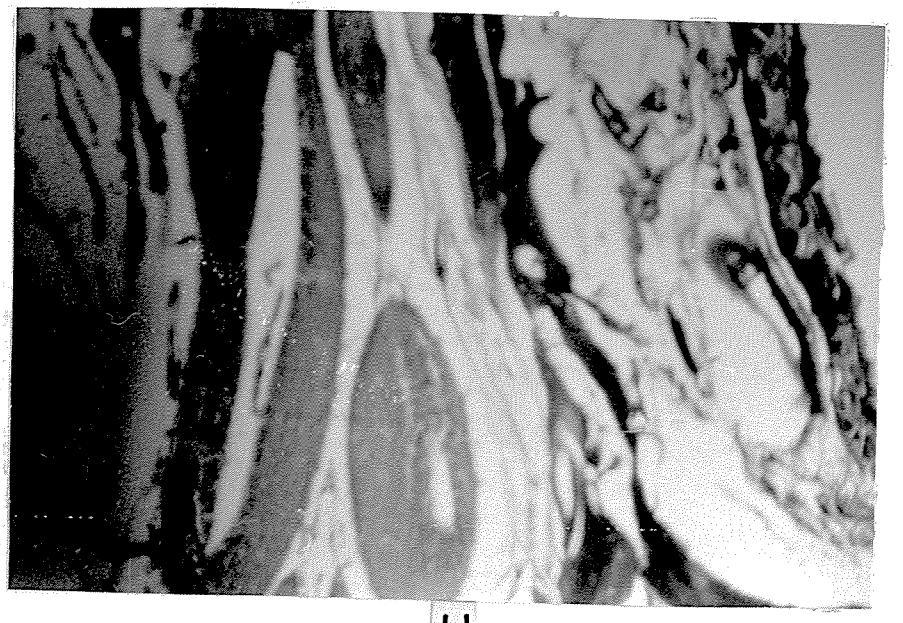
(Explanation of Figures)*

*All figures are photomicrographs.

(Explanation of Figures)

Fig. 11. A horizontal section of the cerebral hemispheres of Triturus viridescens 12 weeks after unilateral incision. Observe the lateral ventricle of the injured hemisphere. X 35.

Fig. 12. A horizontal section of the cerebral hemispheres 12 weeks after unilateral incisions. Observe the extent of the gap and the lateral ventricle of the injured hemisphere. X 35.



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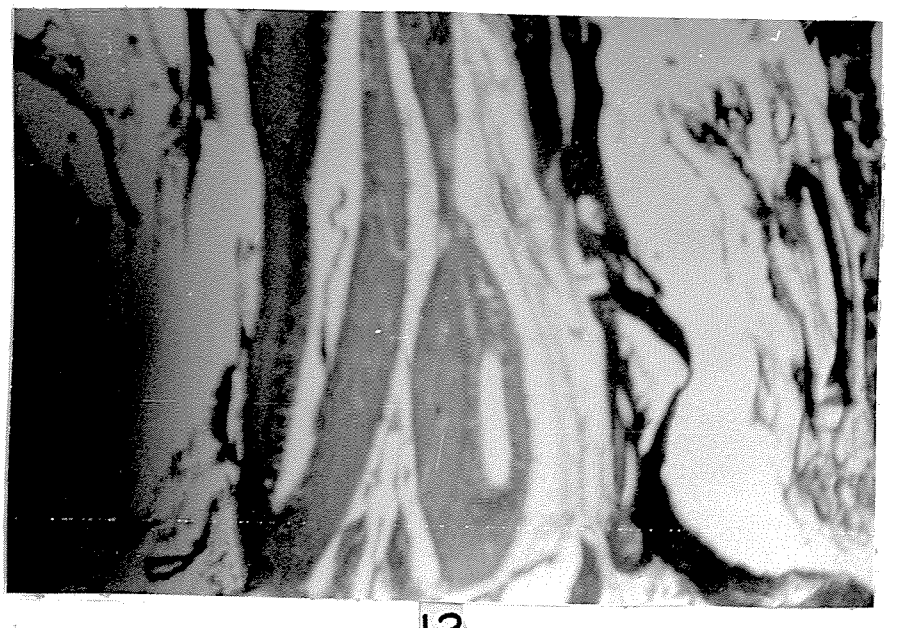

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PLATE VII

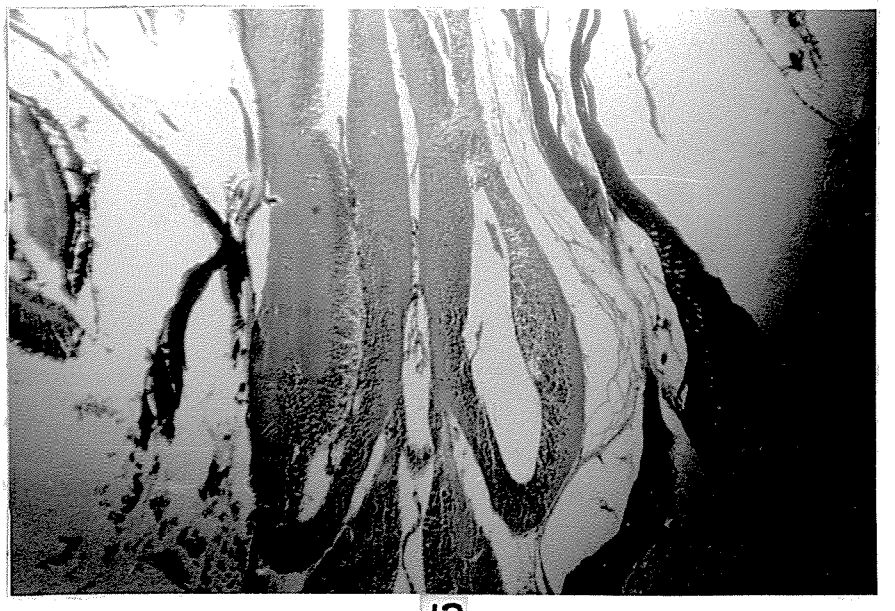
(Explanation of Figures)*

*All figures are photomicrographs.

(Explanation of Figure)

Fig. 13. A horizontal section of the cerebral hemispheres of Triturus viridescens 12 weeks after unilateral incision. Observe the lateral ventricle in the rostral portion of the injured hemisphere. X 35.

Fig. 14. A horizontal section of the cerebral hemispheres 12 weeks after unilateral incision. Observe the lateral ventricle of the injured hemisphere. X 35.



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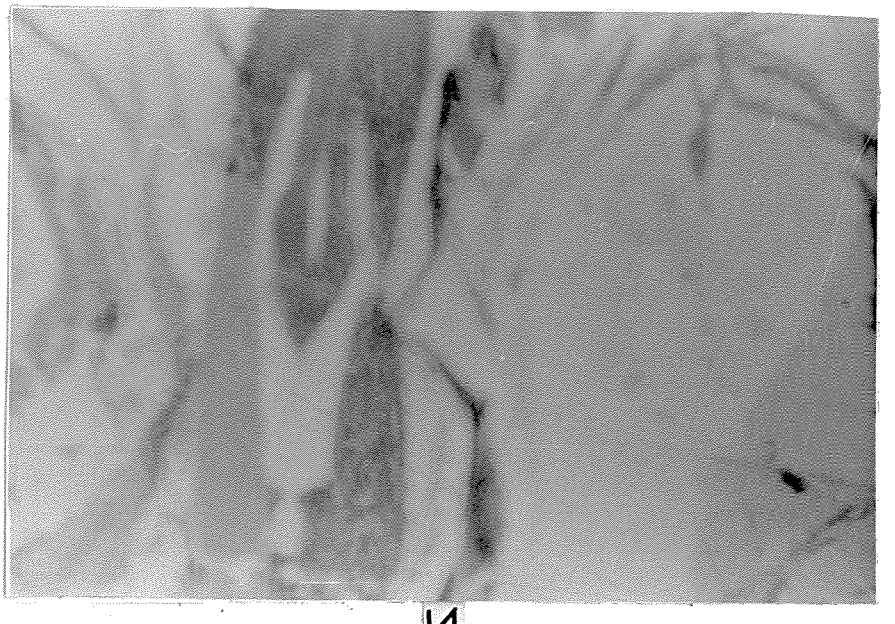

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PLATE VIII

(Explanation of Figures)*

*All figures are photomicrographs.

(Explanation of Figures)

Fig. 15. A horizontal section of the cerebral hemispheres of Triturus viridescens 12 weeks after unilateral incision. Observe the stratum glomerulosum of the injured hemisphere. X 100.

Fig. 16. A horizontal section of the cerebral hemispheres of Triturus viridescens 13 weeks after unilateral incision. Observe the gap in the injured hemisphere. X 100.

15

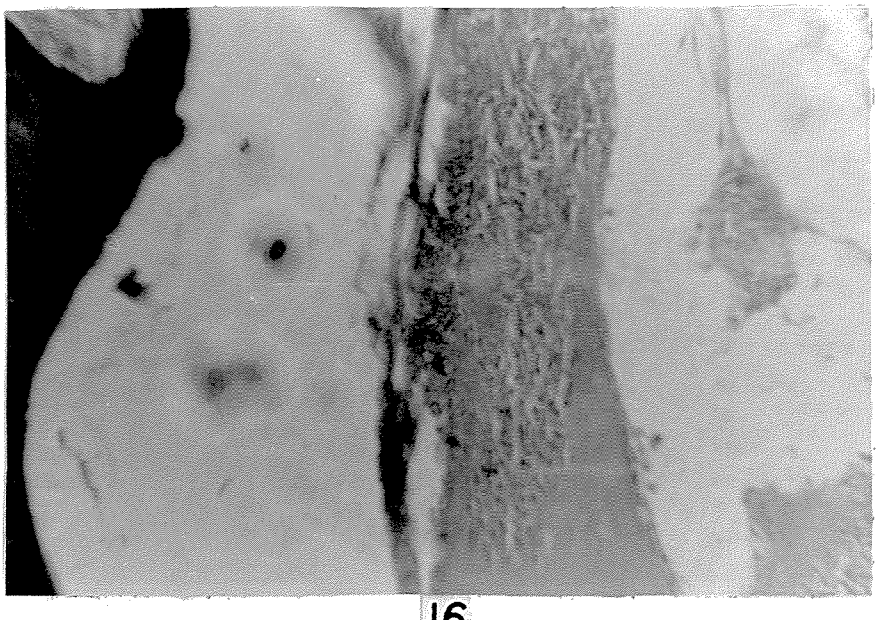

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PLATE IX

(Explanation of Figures)*

*All figures are photomicrographs.

(Explanation of Figures)

Fig. 17. A horizontal section of the cerebral hemispheres of Triturus viridescens 13 weeks after unilateral incision. Observe the olfactory nerve, stratum glomerulosum and the size of the olfactory bulb of the injured hemisphere. X 35.

Fig. 18. A horizontal section of the cerebral hemisphere 13 weeks after unilateral incision. Observe the olfactory bulb of the injured hemisphere and the muscle tissue in the injured area. X 35.

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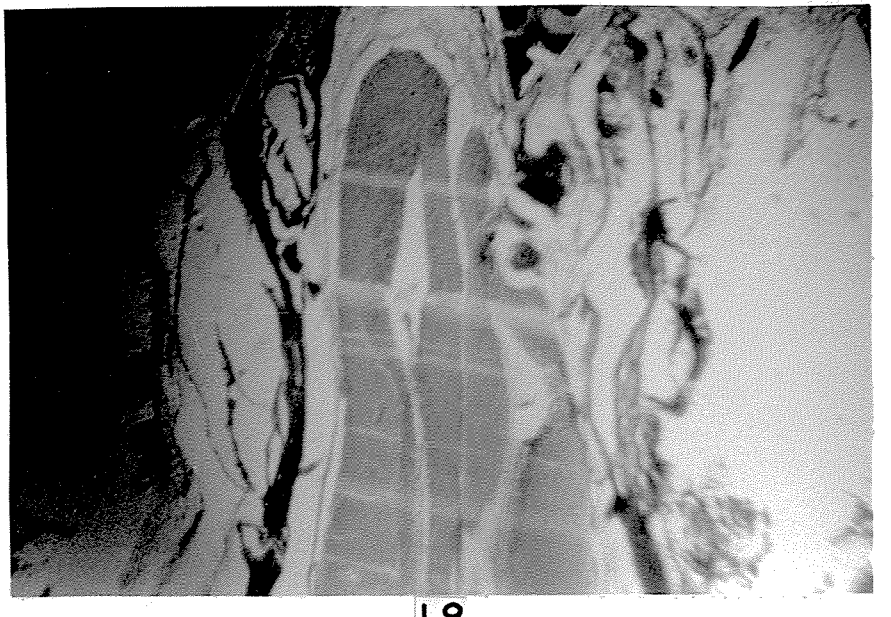

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PLATE X

(Explanation of Figures)*

*All figures are photomicrographs.

(Explanation of Figures)

Fig. 19. A horizontal section of the cerebral hemispheres of Triturus viridescens 13 weeks after unilateral incision. Observe the olfactory bulb of the injured hemisphere. X 35.

Fig. 20. A horizontal section of the cerebral hemispheres 13 weeks after unilateral incision. Observe that the olfactory bulb of the injured side can no longer be seen. X 35.

19

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PLATE XI

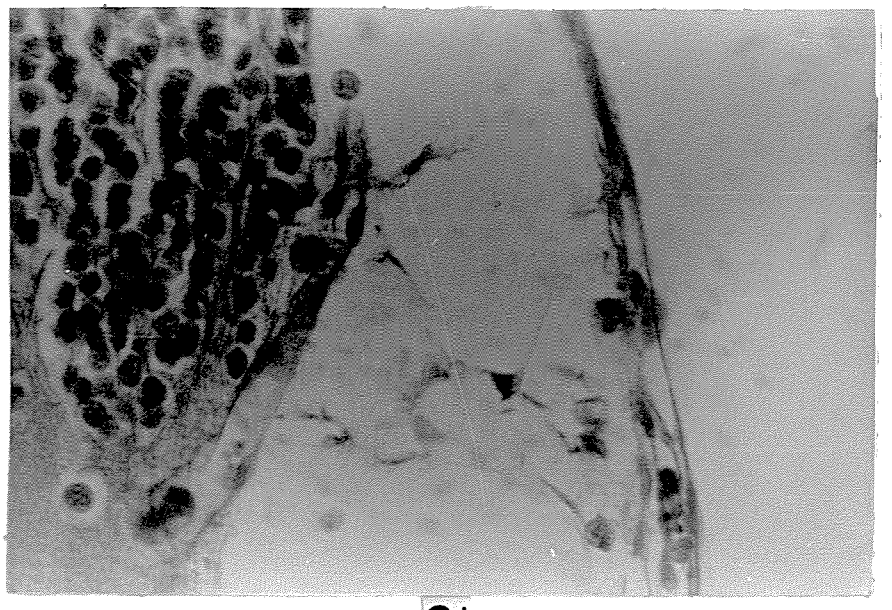
(Explanation of Figures)*

*All figures are photomicrographs.

(Explanation of Figures)

Fig. 21. A horizontal section of the cerebral hemisphere of Triturus viridescens 13 weeks after unilateral incision. Observe the fibers, nerve and neuroglial cells in the injured area. X 430.

Fig. 22. A horizontal section of the injured cerebral hemisphere in an area more dorsal to that shown in fig. 21. Observe the fibers, nerve and neuroglial cells. X 430.



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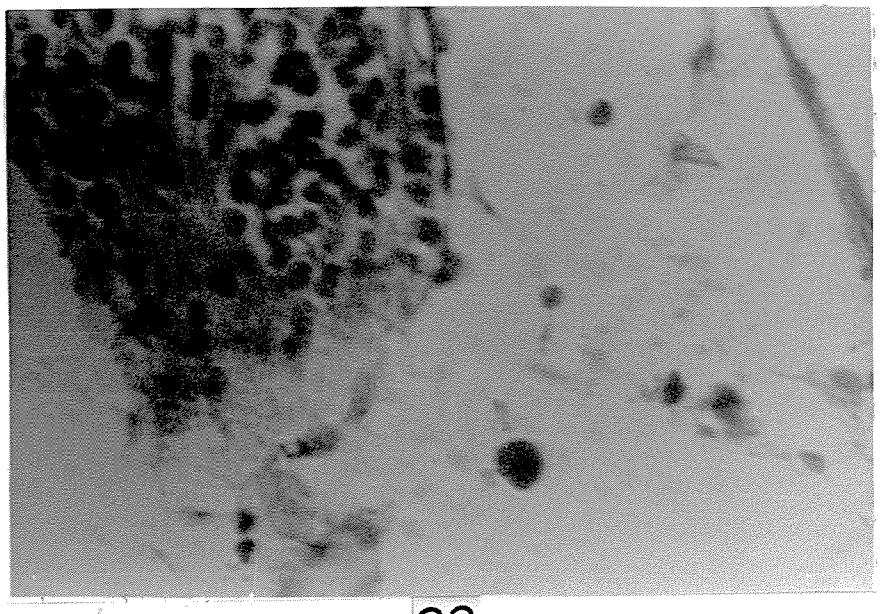

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